Identification and Application of Yield-Related QTLs in Soybean Based on GWAS

Dan Cao, Yongguo Xue, Xiaofei Tang, Jianqiang Sun, Xiaoyan Luan, Qi Liu, Zifei Zhu, Wenjin He, Xinlei Liu ✉

Soybean Research Institute, Heilongjiang Academy of Agricultural Science, Harbin, 150086, Heilongjiang, China

✉ Corresponding email: nkyddslxl@163.com

Abstract This study consolidates and analyzes advancements in identifying yield-related quantitative trait loci (QTLs) in soybean using genome-wide association studies (GWAS). Focusing on methods and outcomes for locating key QTLs that influence soybean yield, this paper summarizes the application of advanced genotyping techniques such as high-density single nucleotide polymorphism (SNP) arrays and whole-genome sequencing, along with the role of machine learning algorithms in improving QTL detection accuracy. The potential of these QTLs in marker-assisted selection (MAS) and genomic selection (GS) is also explored. Additionally, this review highlights the importance of multi-environment trials and candidate gene validation in enhancing QTL applicability, providing a theoretical foundation and technical outlook for high-yield soybean breeding. By synthesizing current findings, this study offers a comprehensive perspective for further genetic research on soybean yield traits and precision breeding strategies.

Keywords Soybean; Genome-wide association studies (GWAS); Quantitative trait loci (QTLs); Marker-assisted selection; Genomic selection; Yield traits; Machine learning

1 Introduction

Soybean (*Glycine max* [L.] Merr.) is one of the most significant crops globally, primarily due to its high oil and protein content, which are essential for human and animal nutrition. It serves as a critical source of edible oil and protein-rich food, making it indispensable in the agricultural sector (Kumar et al., 2021; Rani et al., 2023). The increasing global population and the rising demand for soybean products necessitate the development of improved soybean varieties to ensure food security and meet nutritional needs.

Improving soybean yield is crucial for enhancing agricultural productivity and profitability. Higher yields can help meet the growing demand for soybean products, thereby supporting the agricultural economy and ensuring a stable supply of essential nutrients. However, achieving significant yield improvements is challenging due to the complex genetic interactions and environmental factors that influence soybean growth and development (Kumar et al., 2021; Rani et al., 2023). Therefore, identifying and utilizing genetic factors that contribute to yield enhancement is of paramount importance.

Quantitative trait loci (QTLs) play a vital role in understanding the genetic basis of yield-related traits in crops. QTL mapping and genome-wide association studies (GWAS) are powerful tools for identifying genomic regions associated with important agronomic traits, including yield (Rani et al., 2023; Wang et al., 2023). By pinpointing specific QTLs, researchers can develop molecular markers for marker-assisted selection (MAS), facilitating the breeding of high-yielding soybean varieties. The identification of stable and novel QTLs can significantly contribute to the genetic improvement of soybean, enabling breeders to enhance yield and other desirable traits more efficiently (Huang et al., 2020; Kim et al., 2023).

This study analyzes diverse soybean germplasm resources, consolidating genomic loci associated with key yield-related traits and identifying candidate genes as potential targets for future breeding programs. It aims to provide valuable insights into the genetic factors affecting soybean yield and to support the development of high-yield soybean varieties through marker-assisted selection.

2 Methodological Overview of GWAS in Soybean
2.1 Fundamentals of GWAS in plant breeding
Genome-Wide Association Studies (GWAS) have become a cornerstone in plant breeding, particularly for crops like soybean. GWAS involves scanning the genome of a diverse set of genotypes to identify genetic variations associated with specific traits. This method leverages natural genetic diversity and high-throughput genotyping to link phenotypic traits to genetic loci, facilitating the identification of quantitative trait loci (QTL) that can be used in marker-assisted selection (MAS) (Shook et al., 2021; Priyanatha et al., 2022; Rani et al., 2023).

2.2 Statistical models used in GWAS
Several statistical models are employed in GWAS to account for the complex genetic architecture of traits. Mixed Linear Models (MLM) are commonly used due to their ability to control for population structure and relatedness among individuals, which reduces false positives (Yoosefzadeh-Najafabadi et al., 2021; Rani et al., 2023). Other models like Fixed and Random Model Circulating Probability Unification (FarmCPU) and machine learning algorithms such as Support Vector Regression (SVR) and Random Forest (RF) have also been utilized to enhance the detection power and accuracy of QTL identification (Yoosefzadeh-Najafabadi et al., 2023). Additionally, the environmental interactions for complex traits were not fully explored, which could affect the stability of the identified QTLs across different environments (Figure 1) (Yu et al., 2022).
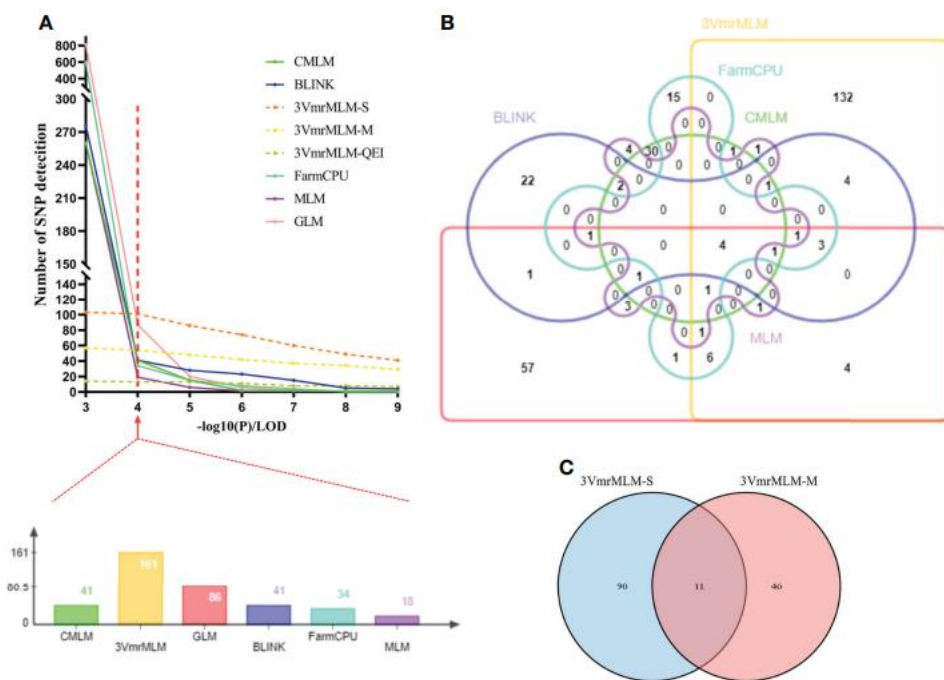

Figure 1 Statistics of QTLs in GWAS results under three models (Adopted from Yu et al., 2022)
Image caption: (A) Statistics on the number of QTLs detected at different significance thresholds by different models or methods. (B)Venn diagram representing the number of unique and shared QTLs with six models. (C) Venn diagram representing the number of unique and shared QTLs with 3VmrMLM single-environment method and 3VmrMLM multiple-environment method. Finally determine the red line (A) represents the GWAS significance threshold of this study, both (B, C) are counted at this significance threshold. 3VmrMLM-S represents 3VmrMLM single-environment method, 3VmrMLM-M represents QTL detection of 3VmrMLM multiple-environment method, 3VmrMLM-QEI represents QEI detection of 3VmrMLM multiple-environment method (Adopted from Yu et al., 2022)

2.3 Genotyping techniques
Genotyping in GWAS can be performed using various techniques, including Single Nucleotide Polymorphism (SNP) arrays and whole-genome sequencing. SNP arrays, such as the SoySNP50K iSelect BeadChip, provide a cost-effective and high-throughput method for genotyping large populations (Ayalew et al., 2022; Rani et al.,

2023). Whole-genome sequencing offers a more comprehensive approach, capturing a broader spectrum of genetic variation, but at a higher cost (Khan et al., 2019; Priyanatha et al., 2022).

2.4 Phenotypic trait data collection
Accurate phenotypic data collection is crucial for the success of GWAS. In soybean, yield and yield-related traits such as seed yield, plant height, seed weight, and pod shattering are commonly measured. These traits are often evaluated across multiple environments to account for genotype-by-environment interactions, which can significantly influence trait expression (Ayalew et al., 2022; Izquierdo et al., 2023). High heritability of traits like seed yield and shattering resistance ensures reliable association mapping (Bhat et al., 2022).

2.5 Challenges in GWAS
GWAS faces several challenges, including population structure, marker density, and environmental effects. Population structure can lead to spurious associations if not properly accounted for, necessitating the use of models like MLM (Yoosefzadeh-Najafabadi et al., 2021; Rani et al., 2023). Marker density is another critical factor; insufficient marker coverage can result in missing important QTL. High-density SNP arrays and whole-genome sequencing help mitigate this issue (Khan et al., 2019; Priyanatha et al., 2022). Environmental effects and genotype-by-environment interactions add another layer of complexity, requiring multi-environment trials to ensure robust QTL detection (Ayalew et al., 2022; Izquierdo et al., 2023). By addressing these challenges and leveraging advanced statistical models and genotyping techniques, GWAS continues to be a powerful tool in identifying yield-related QTLs in soybean, ultimately aiding in the development of improved cultivars.

3 Yield-Related Traits and Their Importance in Soybean
3.1 Key yield-related traits identified in previous studies
Several key yield-related traits have been identified in soybean through various studies. These traits include seed yield per plant (SYP), number of pods per plant, number of seeds per plant, and 100-seed weight (HSW) (Bhat et al., 2022). Additionally, traits such as seed weight, shattering resistance, days to maturity, and plant height have also been highlighted as significant contributors to yield (Ayalew et al., 2022). The identification of these traits is crucial as they directly influence the productivity and overall yield of soybean crops.

3.2 Genetic factors influencing soybean yield
The genetic basis of soybean yield has been extensively studied using genome-wide association studies (GWAS) and quantitative trait loci (QTL) mapping. For instance, a study identified 19 single-nucleotide polymorphisms (SNPs) significantly associated with seed yield, with stable QTLs detected on chromosomes 9 and 17 (Ayalew et al., 2022). Another study revealed 57 SNPs associated with four yield-related traits across multiple environments, identifying six consistent SNPs that were considered stable QTL regions (Bhat et al., 2022). Furthermore, machine learning algorithms have been employed to enhance the discovery of relevant QTLs, demonstrating the potential of sophisticated mathematical approaches in genomic studies (Yoosefzadeh-Najafabadi et al., 2021; Zhang, 2024). These genetic factors are pivotal for marker-assisted selection and breeding programs aimed at improving soybean yield.

3.3 Influence of environment on yield and QTL expression
Environmental factors play a significant role in the expression of yield-related traits and QTLs in soybean. Studies have shown that genotype by environment (GxE) interactions can significantly impact yield stability and the expression of QTLs (Happ et al., 2021). For example, a study identified QTLs for seed yield in both irrigated and rain-fed environments, highlighting the differential responses of yield under varying irrigation conditions (Lee et al., 2021). Another study used a new GWAS model to identify QTL-by-environment interactions (QEIs) for tocopherol content in soybean seed, demonstrating that environmental interactions are often overlooked in traditional GWAS models (Yu et al., 2022). These findings underscore the importance of considering environmental factors in breeding programs to develop high-yielding and stable soybean cultivars. By understanding the key yield-related traits, the genetic factors influencing these traits, and the impact of environmental interactions, researchers can develop more effective strategies for improving soybean yield through targeted breeding and genetic modification (Hina et al., 2020; Zhang et al., 2020).

4 Case Study: GWAS for Identifying Yield-Related QTLs in Soybean

4.1 Research area, environmental conditions, and soybean germplasm

The study was conducted across multiple environments to capture the genotype by environment interactions that significantly influence soybean yield. For instance, one study evaluated 227 soybean genotypes across four different environments (Figure 2) (Yoosefzadeh-Najafabadi et al., 2021), while another assessed 541 genotypes in four environments in Kansas, U.S. (Ayalew et al., 2022). These diverse environmental conditions help in identifying stable QTLs that are consistent across different settings. The germplasm used in these studies included a wide range of soybean genotypes. For example, a panel of 541 soybean genotypes from three maturity groups was used (Ayalew et al., 2022), and another study utilized 200 genotypes derived from Canadian × Chinese crosses (Priyanatha et al., 2022). This diversity in germplasm ensures a broad genetic base, which is crucial for identifying yield-related QTLs.
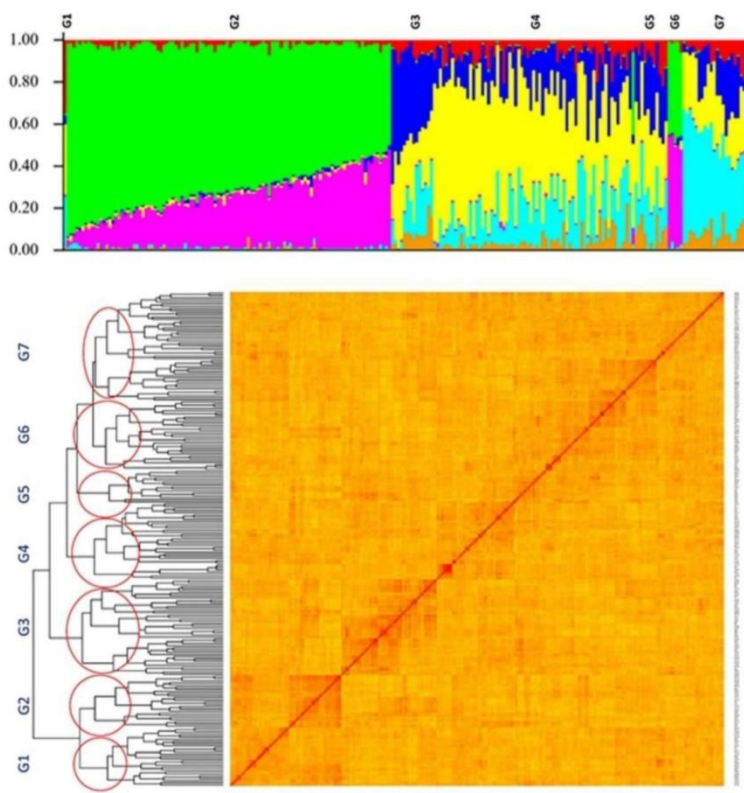

Figure 2 The structure and kinship plots for the 227 soybean genotypes (Adopted from Yoosefzadeh-Najafabadi et al., 2021)

Image caption: The x-axis is the number of genotypes used in this GWAS panel, and the y-axis is the membership of each subgroup. G1-G7 stands for the subpopulation (Adopted from Yoosefzadeh-Najafabadi et al., 2021)

4.2 Genotyping process and measurement of phenotypic traits

Genotyping was performed using high-density SNP arrays and sequencing methods. The SoySNP50K iSelect BeadChip was used to genotype 541 soybean genotypes, identifying 19 significant SNPs associated with seed yield (Izquierdo et al., 2023). Another study employed genotyping-by-sequencing (GBS) to yield almost 32K high-quality SNPs for 200 genotypes. These high-density markers provide comprehensive coverage of the soybean genome, facilitating the identification of QTLs. Phenotypic traits measured included seed yield, seed weight, pod number, and other yield components. For instance, seed yield, seed weight, shattering resistance, days to maturity, and plant height were measured in a diverse panel of soybean genotypes. Another study focused on seed yield, seed protein concentration, seed oil concentration, plant height, 100-seed weight, days to maturity, and lodging score (Shook et al., 2021). These measurements are critical for associating phenotypic traits with genetic markers.

4.3 Statistical analysis, GWAS model, and identification and validation of high-yield QTLs
Various GWAS models were employed to identify yield-related QTLs. The Fixed and Random Model Circulating Probability Unification (FarmCPU) model was used in several studies (Yoosefzadeh-Najafabadi et al., 2021; Priyanatha et al., 2022). Additionally, machine learning algorithms like support vector regression (SVR) and random forest (RF) were compared with conventional methods, showing that SVR-mediated GWAS outperformed others in identifying relevant QTLs (Yoosefzadeh-Najafabadi et al., 2023). These advanced statistical models enhance the power and accuracy of QTL detection.

Several QTLs linked to high-yield traits were identified. For example, two stable seed yield QTLs on chromosomes 9 and 17 were consistently detected across multiple environments. Another study identified five QTL regions controlling seed yield and seed oil and protein content. These QTLs are crucial for understanding the genetic basis of yield and can be targeted in breeding programs (Happ et al., 2021). Validation experiments were conducted to confirm the identified QTLs. For instance, candidate gene analysis surrounding the seed yield QTL on chromosome 9 identified Glyma.09G048900 as a potential gene influencing yield. Similarly, functional annotation of candidate genes supported the relevance of identified QTLs (Wang et al., 2021). These validation steps are essential to ensure the reliability of the GWAS findings.

4.4 Implications for future breeding programs
The identified QTLs have significant implications for future breeding programs. The integration of GWAS with machine learning algorithms provides a robust framework for marker-assisted selection, enabling the development of high-yield soybean varieties (Yoosefzadeh-Najafabadi et al., 2023). The insights gained from these studies can guide breeders in selecting superior genotypes, ultimately improving soybean yield and productivity. By leveraging advanced genotyping techniques, comprehensive phenotypic measurements, and sophisticated statistical models, these studies provide a detailed understanding of the genetic architecture underlying soybean yield. The identified QTLs and candidate genes offer valuable targets for breeding programs aimed at enhancing soybean production.

5 Integration of GWAS Results into Soybean Breeding Programs

5.1 Marker-assisted selection (MAS) for yield improvement
Marker-assisted selection (MAS) leverages identified quantitative trait loci (QTL) to enhance specific traits in crops. In soybean, several studies have identified QTLs associated with yield and other agronomic traits. For instance, a study identified 19 single-nucleotide polymorphisms (SNPs) significantly associated with seed yield, with stable QTLs on chromosomes 9 and 17 (Ayalew et al., 2022). These QTLs can be used to develop markers for MAS, facilitating the introgression of desirable traits into elite soybean lines. Another study highlighted the potential of MAS in improving seed protein and oil content, which are crucial for soybean's nutritional profile (Fields et al., 2023; Wang, 2024). The integration of these markers into breeding programs can significantly enhance yield and quality traits in soybean.

5.2 Genomic selection (GS) and prediction models for yield traits
Genomic selection (GS) uses genome-wide markers to predict the breeding value of individuals, enabling the selection of superior genotypes. Studies have demonstrated the effectiveness of GS in soybean breeding. For example, genomic prediction models using ridge regression best linear unbiased prediction (rrBLUP) have shown high accuracy for traits such as protein content, oil content, and yield (Ravelombola et al., 2021; Qin et al., 2022). Additionally, machine learning algorithms like support vector regression (SVR) have outperformed traditional methods in identifying relevant QTLs for yield components, suggesting their potential in GS (Yoosefzadeh-Najafabadi et al., 2023). These advanced prediction models can accelerate the breeding cycle and improve the efficiency of selecting high-yielding soybean varieties.

5.3 Use of identified QTLs in multi-environment trials
The stability of QTLs across different environments is crucial for their effective use in breeding programs. Multi-environment trials help in identifying QTLs that are consistently associated with yield traits under varying conditions. A meta-GWAS study involving multiple environments identified 483 QTLs, with some loci showing

consistent effects across different studies (Shook et al., 2021). Similarly, another study reported stable QTLs for seed yield in at least three out of four environments, highlighting their robustness (Ayalew et al., 2022). These stable QTLs can be used to develop soybean varieties that perform well across diverse environmental conditions, ensuring reliable yield improvements.

5.4 Challenges and potential solutions for incorporating GWAS findings into breeding

Incorporating GWAS findings into breeding programs presents several challenges, including the complexity of trait inheritance, genotype-environment interactions, and the need for high-throughput phenotyping. One challenge is the limited statistical power of conventional GWAS methods, which can be addressed by integrating machine learning algorithms to enhance QTL detection (Yoosefzadeh-Najafabadi et al., 2021; Yoosefzadeh-Najafabadi et al., 2023). Another challenge is the negative correlation between important traits, such as seed protein and oil content, which requires careful selection strategies to balance these traits (Fields et al., 2023). Additionally, the integration of multi-environment trial data can help identify stable QTLs, reducing the impact of genotype-environment interactions (Shook et al., 2021). By addressing these challenges, breeders can effectively utilize GWAS findings to develop high-yielding, resilient soybean varieties (Stewart-Brown et al., 2019).

6 Concluding Remarks

Looking forward, the application of GWAS in soybean breeding presents numerous opportunities for yield improvement. The continuous refinement of GWAS methodologies, including the incorporation of machine learning techniques, will likely enhance the precision of QTL identification. Future research should focus on validating the identified QTLs and understanding their functional mechanisms to develop more effective breeding strategies. Additionally, expanding the genetic diversity of soybean germplasm panels and conducting multi-environment trials will help identify QTLs that are stable across different conditions, thereby improving the resilience and adaptability of soybean cultivars. The integration of genomic selection (GS) with GWAS also holds promise for accelerating the breeding cycle and achieving higher genetic gains in soybean yield and related traits.

Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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